

Olfactory discrimination of plant volatiles by the European starling

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Abstract. Passerine species that re-use nest sites often incorporate fresh green vegetation into their nests, a behaviour consistent with the possibility that some birds may use chemical properties of plants to counteract the selective potential of parasites and pathogens. We tested adult starlings (*Sturnus vulgaris*) for their physiological capacity and behavioural ability to detect and discriminate between volatiles emitted from plant material. Multi-unit electrophysiological recordings from olfactory nerves of adults indicated that strong responses were reliably elicited by volatiles from six plant species. After pairings of plant volatiles with gastro-intestinal malaise, birds exhibited conditioned avoidance in behavioural experiments, and made all possible pairwise discriminations between volatiles of the various plant species. Bilateral olfactory nerve cuts prior to conditioning abolished the ability to acquire avoidance, suggesting that olfactory cues mediated the response to plant species. These and previous results suggest that starlings use volatile cues to discriminate and choose between plants used in nest construction.

The significance of fresh vegetation incorporated into a dry nest matrix has been a subject of speculation (Collias & Collias 1984). Four major hypotheses have emerged as explanations for the utility of this behaviour: birds may incorporate vegetation (1) to conceal their nest from the view of predators; (2) to regulate the humidity of the nest environment, presumably to alter the desiccation rate of the eggs; (3) to influence the heat flux dynamics of the nest and its occupants; and (4) to fumigate the nest via the chemical compounds contained therein and ameliorate the effects of parasites and pathogens against eggs or young. The degree to which any or all of these hypotheses influence the life history of passerines is largely unknown.

We have been studying vegetation preferences demonstrated by the European starling, *Sturnus vulgaris*, and the biological activity of the plants as related to the fumigant hypothesis (Clark & Mason 1985). Briefly, we found that starlings selected fresh vegetation with high biocidal potential relative to available plants in the habitat, and that these plants possess more volatiles at higher concentrations relative to other available plants. Because volatiles were implicated as the primary biocidal agents, we hypothesized that starlings might use chemical cues as one source of information for selecting appropriate plants during nest construction. Chemical

cues would provide an excellent index for this purpose because they may be correlated with the concentration of biocides, while leaf shape or colour may not (Clark & Mason 1985). This paper reflects a partial test of the criterion that passerines are able to utilize volatile (e.g. olfactory) cues as one basis for selecting fresh plant material used during nest construction.

Many, if not all, species of bird possess the requisite anatomical structures and neurophysiological capacity to perceive volatile (e.g. olfactory) cues (Tucker 1965; Bang & Cobb 1968; Bang 1971). The ability of birds to perceive odour behaviourally has also been empirically supported both in the laboratory (Michelsen 1959; Wenzel 1973) and under field conditions (Grubb 1972; Wenzel 1972). Nonetheless, many biologists are still reluctant to credit birds, as a group, with an acute sense of smell.

Because of the small size of their olfactory bulbs relative to other orders of birds, passerines are commonly assumed to possess the poorest olfactory ability. To determine the olfactory abilities of starlings we (1) obtained integrated multi-unit responses from the olfactory nerves of five adult birds as evidence of peripheral olfactory capacity, (2) determined whether starlings could be conditioned to discriminate between plants using volatile cues alone, and (3) determined whether such

discrimination was based upon olfaction rather than other chemical senses.

METHODS

Experiment 1: Peripheral Olfactory Capacity

Five adult starlings were decoy-trapped at Sandusky, Ohio and were used for electrophysiology experiments. In the laboratory, individuals were anaesthetized with Urethane (2.0 ml/kg intraperitoneally), secured in a head-holder apparatus, and the inter-orbital cavity was surgically exposed. Bonewax was packed into the cavity to seal it off from the air passages, while a small teflon cap was fixed to the skull with powdered dental adhesive and distilled water so as to form a reservoir. Mineral oil was pipetted into the reservoir to prevent desiccation of the nerve and to provide electrical insulation. The olfactory nerves under the bony orbital walls were exposed and the outer membrane sheath surrounding the nerves was removed. Electrical activity from anaesthetized birds was recorded from the left olfactory nerve by teasing free a small twig and placing it on a pair of platinum-iridium wire electrodes. The preparation was grounded to the head-holder apparatus. The platinum-iridium electrodes were connected to a high impedance probe on an AC preamplifier and the amplified output was monitored on a storage oscilloscope and audio monitor. Neural activity was summated using a leaky integrator (i.e. short-time averaging circuit with a time constant of 0.5–1.0 s) and was displayed on a chart recorder (Kiyohara & Tucker 1978). The magnitude of the integrated neural response was proportional to the number of nerve pulses per unit time and was measured in arbitrary units from baseline to the peak of the phasic response. Responses were recorded as a percentage of the neural response to an arbitrarily selected standard stimulus, air saturated with *n*-butanol (AR Grade, Eastman Kodak) at 23°C.

Eight stimuli were presented to each bird: a control (ambient air passed through the delivery apparatus), the standard (*n*-butanol), and volatiles from the leaves of six species of plants. Four of the species were commonly preferred by starlings as nest material: agrimony, *Agrimonia paraflorea*, yarrow, *Achillea millefolium*, elm-leaved goldenrod, *Solidago ulmiflora*, and rough goldenrod, *Solidago rugosa*; and two species were not preferred as

nesting material: crooked-stem aster, *Aster prenanthoides*, and willow aster, *Aster praealtus* (Clark & Mason 1985). Two grams of plant material were placed in a 125-ml flask and the volatiles were allowed to accumulate in the head-space of the flask for 15 min. Fifty ml of air from the head-space were delivered to a bird's left external nares at a rate of 10 ml/s. The inter-stimulus interval was 5 min, and the interval between each series of stimuli was 20 min.

Experiment 2: Discrimination Between Plant Volatiles

Adult starlings were decoy-trapped during the first week of December 1983 at Sandusky, Ohio. During the third week of December, the birds were brought to the laboratory and housed, four birds to a cage, in a room with an ambient temperature of 23°C and a 10:14 light:dark cycle. Water was always available, and before the experiments began the birds were permitted to feed ad libitum on Purina Flight Bird Conditioner. After 2 weeks, 20 birds were randomly selected, individually housed, and visually isolated. Seven days later, the birds were given 1 week of adaptation to a food deprivation regime. On each day of adaptation the birds were food-deprived 2 h before the end of the light cycle. On the next day, 1 h after the onset of the light cycle, they were allowed to feed from a cup containing 20 g of food. Each cup was covered by a metal lid with a circular opening (3.2 cm diameter) in the centre. Beneath the food, covered by a nearly opaque nylon-mesh screen, was 2 g of fresh plant material. The screen prevented the birds from seeing or contacting the plant material. To feed, starlings had to insert their beaks into the food cup and into the head-space which contained odours from the plant. The aim of including plant materials in food cups during adaptation was to control for the possibility of neophobic responses during subsequent conditioning and testing phases of the experiments. Blue field madder, *Sherardia arvensis*, was used as the adaptation plant for all trials. After 1 h, the food cups were removed, and food consumption was recorded. Spillage was not recorded, since in previous work it merely reflected consumption (Mason & Reidinger 1983). The birds were then permitted ad libitum access to food for the remainder of the light period.

On the day following the last day of adaptation to deprivation, the starlings were ranked according

Table I. A list of plants and codes used during the experiments

Code	Family	Binomial	Common name
Agrpar	Rosaceae	<i>Agrimonia paraflorea</i>	Agrimony
Geucan		<i>Geum canadense</i>	White avens
Potrec		<i>Potentilla recta</i>	Rough-fruited cinquefoil
Achmil	Asteraceae	<i>Achillea millefolium</i>	Yarrow
Astpra		<i>Aster praealtus</i>	Willow aster
Astpre		<i>Aster prenanthoides</i>	Crooked-stem aster
Erisp		<i>Erigeron</i> species	Fleabane
Solrug		<i>Solidago rugosa</i>	Rough goldenrod
Solulm	Cruciferae	<i>Solidago ulmiflora</i>	Elm-leaved goldenrod
Alloff		<i>Alliaria officinalis</i>	Garlic mustard
Barvul		<i>Barbarea vulgaris</i>	Winter cress
Branig		<i>Brassica nigra</i>	Black mustard
Daucar	Umbelliferae	<i>Daucus carota</i>	Wild carrot
Glehed	Labiatae	<i>Glechoma hederacea</i>	Gill-over-the-ground
Lampur		<i>Lamium purpureum</i>	Purple dead-nettle
Polrep	Polemoniaceae	<i>Polemonium reptans</i>	Greek valarian
Plamaj	Plantaginaceae	<i>Plantago major</i>	Common plantain
Rancan	Ranunculaceae	<i>Ranunculus canadensis</i>	Buttercup

to mean consumption during the morning hourly period, and assigned to four groups ($N=5$ per group) that were balanced with respect to food intake. The next morning, two groups were exposed to volatiles (conditioned stimulus; CS) from a second plant species (B), and two groups were exposed to volatiles (CS) from a third plant species (C) as described above (see Table I for a list of plants used). After 1h, the food cups were removed from the cages. One group exposed to species B, and one group exposed to species C were gavaged (oesophageally intubated) with a methiocarb/propylene glycol solution (2 mg/kg). The remaining groups were gavaged with propylene glycol alone (2 ml/kg). Methiocarb, a bird repellent, produces conditioned avoidance in birds similar to that produced by lithium chloride (Mason & Reidinger 1983; Mason & Silver 1983). Gavages were completed within 15 min of the end of the conditioning trial. Plain food cups (without plant material) were returned to the cages 1 h later, and the birds were left undisturbed for the remaining hours of light with ad libitum access to food. On each of the 5 days immediately following the day of conditioning, all birds were given 1h two-choice tests between food paired with volatiles from plants B or C.

Suppression ratios were calculated by dividing the consumption of food paired with the CS by the total consumption, i.e. food paired with both the

respective CS and the alternative plant volatile. Suppression ratios were interpreted as an index of a conditioned avoidance feeding response formed by starlings. Within a two-choice test, a ratio of zero indicated that a bird did not consume any food paired with the CS relative to consumption of food paired with volatiles from the alternative plant. A ratio of 0.5 indicated indifference in the relative consumption of food paired with the CS or the alternative plant volatile. A ratio of one indicated a bird consumed only food paired with the CS and no food paired with the alternative plant volatile. Ratios were assessed using a three-way factorial analysis of variance. The CS effect ($df=1$) tested the hypothesis that there was no difference between the mean consumption of food associated with the CS (for volatiles arising from plants B versus C). The treatment effect ($df=1$) tested the hypothesis that there was no difference between the mean consumption of food associated with the gavage (methiocarb plus propylene glycol versus propylene glycol alone). The days effect ($df=4$) represented a repeated measure on individuals for the 5 days post-gavage, and tested the hypothesis that mean consumption between days did not differ. The error term used to test the main and interaction effects of treatment and CS was the 'individuals nested within the treatment-CS' term ($df=16$). Alternatively, the error term used to test the main effect day and its interaction with treatment and CS

was the 'individual-day nested within treatment-CS' term ($df=48$; Winer 1971).

Because each series of odour discrimination tests was carried out independently over an 8-month period, we combined the exact tail probabilities from all eight experiments as a general test for main and interaction effects, rather than treat each experiment as a block effect (Sokal & Rohlf 1981). Such treatment of the data allowed us to make general statements about the relative suppression scores of birds under the conditions of our experimental paradigm.

Experiment 3: Olfactory Discrimination of Plants

Of 20 starlings selected for surgery, 10 were randomly assigned bilateral olfactory nerve cuts (group O) and 10 were assigned sham surgeries (group S). Group O starlings were lightly anaesthetized with Equithesin (2 ml/kg, intra-peritoneally) and placed in a head-holder. The olfactory nerves lying under the bony orbital walls were exposed and a 2-mm section of the olfactory nerve was removed. The cut ends of the nerves were folded back, the cavity packed with Gelfoam, and the skin closed with cyanoacrylate glue (Mason & Silver 1983). Group S birds were treated similarly, except that the nerves were not disturbed. All but one (sham) of the birds recovered within 1 h of surgery.

Two days following surgery, birds were adapted to volatiles from Greek valerian, *Polemonium reptans*, during feeding trials, and subsequently conditioned to volatiles (CS) from either a fleabane species, *Erigeron*, or rough-fruited cinquefoil, *Potentilla recta*. This was done inadvertently and resulted in 2–3 birds per treatment cell. For the purpose of analysis, because of the cell sample size, we collapsed 'birds' over 'plants', despite the knowledge that asymmetries in the response to plants serving as the CS were likely to add to the experimental error term. Nineteen days after the surgeries we repeated the experiments, adapting the birds to black mustard, *Brassica nigra*, and subsequently conditioning all birds to volatiles (CS) from red-dead nettle, *Lamium purpureum*. Birds were subsequently given two-choice tests between *L. purpureum* and a third plant, garlic mustard, *Alliaria officinalis*.

Suppression ratios were analysed using a three-way factorial analysis of variance. The main effect of surgery (sham or olfactory nerve cut) and treatment (methiocarb or control gavage) and their

interaction were tested for significance using the 'subjects within surgery-treatment' term. The main effect of day and its interactions with surgery and treatment were tested for significance using the 'subject-day nested within surgery-treatment' term (Winer 1971).

RESULTS AND DISCUSSION

Experiment 1: Peripheral Olfactory Capacity

Multi-unit responses were obtained to presentations of *n*-butanol and plant volatiles (Fig. 1). *n*-Butanol elicited the strongest absolute response. The relative responses to the unscented control and the volatiles from six species of plants were not similar ($F_{6,24}=12.95$, $P<0.001$). Volatiles from all the plants evoked stronger relative responses than the control, while *S. ulmiflora* and *A. prenanthoides* evoked significantly larger relative responses than *A. paraflora* ($P<0.01$, Neuman-Keuls test). No other comparisons between the ranked, mean relative responses differed significantly.

No inference can be made concerning receptor sensitivity on the basis of our results (stimulus

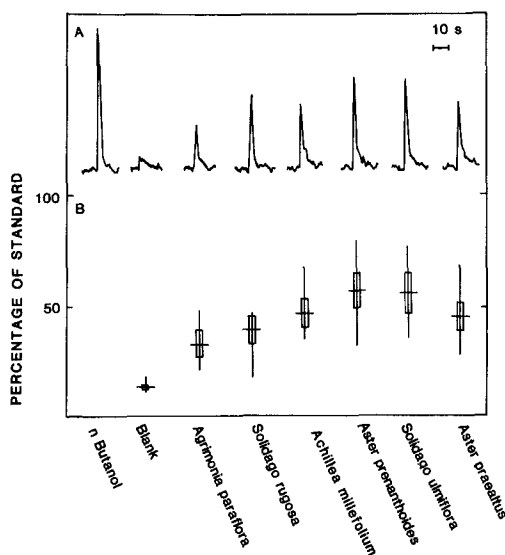


Figure 1. (A) Representative multi-unit olfactory nerve twig recordings from an adult male starling, measured in arbitrary units. (B) Mean (horizontal bar) multi-unit response to odorants derived from plant material relative to *n*-butanol for five adult starlings (two males, three females). Vertical box depicts \pm SE. Vertical line depicts range.

concentration and composition, and respiratory cycle were not controlled). Nevertheless, our findings clearly demonstrate that starlings possess the peripheral olfactory capability to detect plant volatiles. This is the case even though starlings (1) lack any obvious elaboration or specific adaptation of the olfactory apparatus for perception (cf. Tucker 1965; see Bang 1971), and (2) possess an olfactory bulb to ipsilateral cerebellar ratio that is the mean for passerines, a group of birds thought to have poor olfactory ability (Bang & Cobb 1968; Bang 1971).

Experiment 2: Discrimination Between Plant Volatiles

To assess whether starlings had the capacity to detect and discriminate between plant volatiles, birds were conditioned to avoid volatiles associated with food and gastro-intestinal malaise. Subse-

quently, the birds were presented with two food cups, one containing the plant-food combination associated with sickness and the other containing an alternative combination.

The summary statistics based upon the suppression ratio scores for eight independent two-choice discrimination tests are presented in Table II. Inspection of Table II indicates that a large variability exists for factor effects. We attribute the variable responses among factors over the eight experiments to the varying similarity of the chemical composition found between pairings of plants. Some plants may serve as a source for a stronger and/or more identifiable cue for conditioning. Nonetheless, birds demonstrated stronger avoidance learning when treated with methiocarb than when compared to controls for seven of eight of the experiments (Table II, combined probability of the treatment effect was $\chi^2 = 93.19$, $df = 16$, $P < 0.001$). This significant treatment effect can be clearly seen

Table II. *F* values for eight independent odour discrimination experiments

Experiment	Source							
	T	CS	T × CS	D	T × D	CS × D	T × CS × D	
Agrpar versus Potrec	<i>F</i> 23.23	0.56	0.43	2.55	1.20	0.05	1.33	
Achmil versus Branig	<i>P</i> 0.001	0.464	0.530	0.067	0.321	0.986	0.277	
Glehed versus Rancan	<i>F</i> 17.05	3.82	2.97	1.01	0.86	0.66	3.52	
Glehed versus Geucan	<i>P</i> 0.001	0.068	0.104	0.407	0.495	0.619	0.012	
Solrug versus Lampur	<i>F</i> 7.19	10.66	0.80	4.27	4.06	2.54	1.45	
Plamaj versus Daucar	<i>P</i> 0.016	0.005	0.385	0.004	0.005	0.048	0.228	
Barvul versus Erisp	<i>F</i> 0.23	4.01	10.20	2.53	1.56	4.40	1.50	
Polrep versus Solrug	<i>P</i> 0.641	0.063	0.006	0.049	0.197	0.003	0.214	
Alloff	<i>F</i> 19.98	0.28	0.08	0.41	4.11	9.89	1.57	
	<i>P</i> 0.001	0.606	0.783	0.799	0.005	0.001	0.193	
	<i>F</i> 10.90	0.53	0.25	3.29	1.93	4.11	3.02	
	<i>P</i> 0.005	0.476	0.624	0.016	0.117	0.005	0.024	
	<i>F</i> 6.78	0.00	0.48	4.31	2.24	0.61	1.49	
	<i>P</i> 0.019	0.971	0.497	0.009	0.095	0.613	0.229	
	<i>F</i> 30.44	0.33	5.68	1.44	2.75	2.86	1.34	
	<i>P</i> 0.001	0.575	0.029	0.233	0.036	0.031	0.263	

The plant codes are defined in Table I. T represents the gavage treatment (methiocarb versus control), CS represents the conditioned stimulus (source of plant volatiles used for conditioning) and D represents trials (days post-gavage).

P is the probability obtained for the *F* statistic.

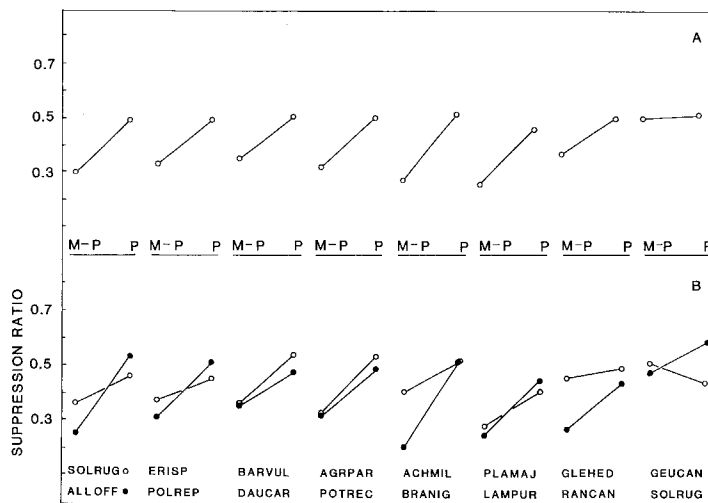


Figure 2. Profiles of mean suppression ratios for eight independent two-choice discrimination tests. The gavage treatment level is indicated in the middle of the figure. M-P is the methiocarb-in-propylene glycol gavage which caused gastro-intestinal malaise in birds. P is the control gavage (propylene glycol alone). Pairs of plants used in the discrimination trials are indicated in code at the bottom of the figure (see Table I for code labels). (A) depicts the mean suppression ratios for the main effect treatment, for pairs of plants in each experiment (open circles); (B), the treatment-CS (conditioned stimulus) interaction, depicts suppression ratios for the CS for each of the species of a plant pair. Open (top row of plants) and closed (bottom row of plants) circles indicate what species the CS is.

from the profiles depicted in Fig. 2A. Along similar lines, Fig. 2B illustrates that birds treated with methiocarb formed stronger conditioned aversions, regardless of which plant in a pair was used as the source of volatiles for the CS, i.e. CS-treatment interaction. Birds within the control treatments consumed food paired with the CS and the alternative plant odour in equal amounts (overall suppression ratio = 0.49, $z = 0.49$, $P = 0.31$), while birds gavaged with methiocarb had a calculated suppression ratio significantly below a value of 0.5, i.e. indifference (overall suppression ratio = 0.36, $z = 4.59$, $P < 0.001$).

While these behavioural results show that starlings can acquire conditioned avoidance of plant volatiles and can discriminate between such volatiles, they do not demonstrate whether such responding is mediated by olfactory cues. No vomeronasal organ or accessory olfactory bulb has been found in birds (Portman 1961), but the existence of septal organs and terminal nerves is controversial (Bang & Wenzel, in press). Certainly, passerines, and starlings in particular, possess functional nasotrigeminal systems (Mason & Silver 1983), and conceivably, plant volatiles in the present study could have been trigeminal, rather

than olfactory stimulants. Experiment 3 was performed to test this possibility. This final experiment was a replication of experiment 2, with the exception that birds were given either bilateral olfactory nerve cuts or sham surgeries prior to conditioning.

Experiment 3: Olfactory Discrimination of Plants

To test the hypothesis that birds used olfactory cues as a basis for discrimination in two-choice tests, we surgically rendered a group of birds anosmic. Groups of anosmic birds (those treated with methiocarb, OM and the controls, OP) were indifferent to the CS, yielding mean suppression ratios of 0.51 and 0.56, respectively for the *Erigeron-Potentilla* two-choice tests. Similarly, the OM and OP groups of the *Lamium-Alliaria* trials produced mean suppression ratios suggesting indifference (0.45 and 0.50, respectively). Birds receiving sham surgery and gavaged with propylene glycol (controls, SP) were also indifferent to the CS. Means for the *Erigeron-Potentilla* and *Lamium-Alliaria* trials were 0.41 and 0.55, respectively. Figure 3 illustrates that only those birds treated with methiocarb and possessing intact olfactory nerves (SM) exhibited strong conditioned avoid-

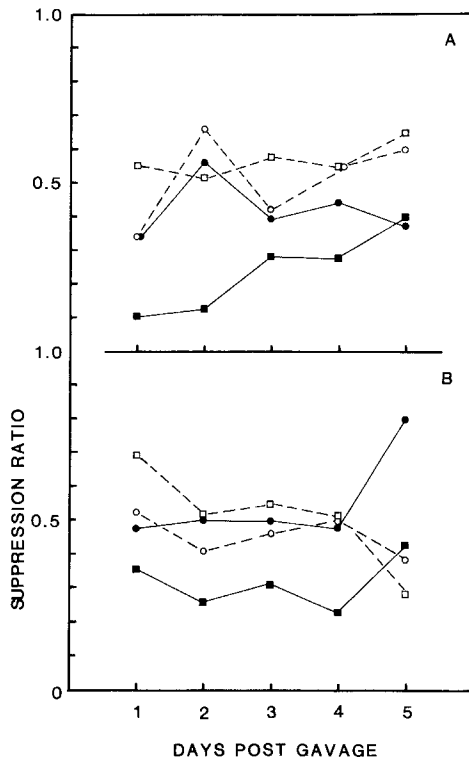


Figure 3. Mean suppression ratios from two-choice tests between (A) *Erigeron* species and *Potentilla recta*, and (B) *Lamium purpureum* and *Alliaria officinalis*. The four treatment groups were: bilateral olfactory nerve cuts with methiocarb treatment (open circle); bilateral olfactory nerve cuts with propylene glycol treatment (open square); sham surgery with methiocarb treatment (closed square); and sham surgery with propylene glycol treatment (closed circle).

ance (combined probability for the surgery-treatment effect for both experiments was $\chi^2=9.73$, $df=4$, $P<0.05$), indicating that starlings can use olfaction as a cue to discriminate between two plants. The mean suppression ratios for the SM groups were 0.24 and 0.32 for the *Erigeron*–*Potentilla* and *Lamium*–*Alliaria* two-choice tests, respectively.

GENERAL DISCUSSION

Increasingly, evidence indicates that olfaction serves an important function in the life history of birds. Most cases of documented olfactory function in field studies of birds focus on their ability to

locate food (Stager 1964; Wenzel 1972; Jouventin 1977; Moshe & Yom-Tov 1978; Wurdinger 1979; Hutchison et al. 1984). There is also evidence to suggest that birds use olfaction as one cue in orientation (Benvenuti et al. 1973; Grubb 1974). Still other evidence suggests some birds use olfaction to mediate pheromonal cues during courtship (Balthazart & Schoffeniels 1979), much as the vomeronasal organ does in mammals.

In most of the cases cited above, the birds studied have a well developed olfactory anatomy (Bang 1971; Wenzel, in press) in addition to documented behavioural and physiological threshold sensitivity to odorants (Tucker 1965; Henton et al. 1966; Wenzel & Sieck 1972; Snyder & Peterson 1979). However, passerines with their small and sometimes fused olfactory bulbs, and a general lack of elaboration of the nasal passages, have been assumed to possess relatively poor olfactory abilities. Yet our data on starlings and those of Tucker (1965) on house sparrows, *Passer domesticus*, suggest that despite the apparent anatomical short-comings, at least two passerines have well-developed olfactory capacities. Whether or not starlings utilize their olfactory ability in the field to select among plants in order to protect their nests chemically remains to be determined.

Birds breeding at sites previously used for nesting by other individuals (e.g. secondary cavity nesting species) incur a greater likelihood of heavy parasite infestation and pathogen infection (Stoner 1936; Rothschild & Clay 1957; Wasyluk 1971). Both have negative effects on the reproductive output and survival of breeding adults (Rettger 1913; Neff 1945; Szybalski 1950; Moss & Camin 1971; Feare 1976; Hoogland & Sherman 1976; Powlesland 1977; Duffy 1983; Gold & Dahlsten 1983; Whiteman & Bickford 1983; Arendt 1985). Meyers (1922), Johnston & Hardy (1962), and Sengupta (1981) postulated that chemicals contained in plants might serve as effective biocides against parasites and pathogens. On the basis of literature reviews, Wimberger (1984) and Clark & Mason (1985) presented evidence that falconiforms and passerines that bred at historically active sites were more likely to incorporate fresh vegetation into their nests. Additionally, Clark & Mason (1985) presented empirical evidence that one secondary cavity nesting species, the starling, selected fresh vegetation from the breeding habitat in a non-random fashion. Plants preferred by starlings were also more effective as biocides against ectoparasites

and pathogens relative to a random subset of non-preferred vegetation.

Although we do not know how starlings acquire their preferences for vegetation, we do know that such preferences vary as a function of the seasonal availability of plants (personal observation) and their local availability (in England: P. Greig-Smith, personal communication; in Ohio: R.A. Dolbeer, personal communication). In selecting green plant material for nest construction, visual cues could be important for the initial location of appropriate plant material. Many plants available to starlings occur in discrete clumps, easily seen by human observers from a distance. However, once a starling is within a patch of vegetation, visual cues are likely to be less important. Visual cues such as leaf shape, size, or colour, may correlate less well with biocidal properties of plants than do the bouquets of emitted volatiles. Furthermore, while there are characteristic chemical differences between plant species that do correlate with external morphological traits (Parks 1974), there is still sufficient chemical variation between individuals of a species to suggest that visual discrimination between individuals is an inadequate basis for the selection of biocidally active leaves (Rosenthal & Janzen 1979). Differences in chemical profiles of individual plants or plant parts often reflect differential expression of chemical defences in response to recent herbivory or pathogen infection.

Starlings do not immediately select a leaf once they enter a patch of vegetation, but spend some non-foraging time searching within the patch (personal observation). At ground level, starlings and plants are within the boundary layer of the wind profile. Volatiles emitted from plants would be at their highest concentrations at this level, an analogous situation to the odour discrimination trials of our experimental design. We speculate that starlings are evaluating chemical cues in the odour plumes within the boundary conditions when they are close to specific plants. It may be unlikely that starlings are discriminating between plants based upon specific chemical products produced by plants. Rather, we suggest that starlings use general volatility as a cue for selecting plants or plant parts. Because more odorous plants tend to contain more compounds at higher concentrations, starlings may increase their chances of encountering biocidal compounds (Clark & Mason 1985) by using chemical cues (e.g. olfaction) to select green plant material for nest construction.

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